

AQUATIC PARAMETERS AND LIFE HISTORY OBSERVATIONS OF THE GREAT BASIN SPADEFOOT TOAD IN UTAH

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ABSTRACT.— The distribution and breeding habitats of the Great Basin spadefoot toad (*Scaphiopus intermontanus*) were investigated in the Bonneville Basin of western Utah. The permanent springs and man-made reservoirs used for breeding were largely found below the 1600 m elevation. The pH's ranged between 7.2 and 10.4 and the total dissolved solids between 170 and 4800 mg/l. The springs were less alkaline than the rain-filled reservoirs. The lack of aquatic vegetation was a common feature of the reservoirs and most of the springs. Observations of breeding without rain are noted as well as the lack of breeding with rain. The snout-vent lengths of adult spadefoots are greater in the Bonneville Basin than in other parts of the Great Basin. Utilization of permanent water sources and stimuli for emergence and breeding, as well as the larger adult size of *S. intermontanus* in the Bonneville Basin, are discussed in relation to the diverse precipitation patterns, the sparseness of the water sources, and the Holocene history of the Great Basin.

Spadefoot toads have been extensively studied in California, Arizona, New Mexico, Texas, and Oklahoma. Very little information is available for the Great Basin spadefoot toad (*Scaphiopus intermontanus*). Tanner (1931) found *S. intermontanus* widely distributed in Utah. Most observations in Utah have been within the Colorado River drainage (Tanner 1931, Hardy 1938, Wood 1935, Wright and Wright 1949). Observations of *S. intermontanus* in the Great Basin ecosystem are less frequent. Tanner (1931) found spadefoots common along the Wasatch Front and reported observations near Gandy and Callao in Utah, near the Nevada border. Synder (1920), Linsdale (1938), and La Rivers (1942) reported the records for Nevada. *Scaphiopus intermontanus* has several unique features that are not found in other spadefoot species: (1) breeding is reported to occur without rainfall for stimulus (Linsdale 1938), (2) a large number of chorusing adults is not essential for breeding (Wood 1935, Blair 1956), and (3) permanent water can be utilized for breeding (Bragg 1961).

This study describes the breeding habitat of *S. intermontanus* in the Bonneville Basin of the Great Basin in western Utah, which is

bounded by the ancient shoreline of Lake Bonneville, a lake that desiccated some 11,000 years ago (Currey 1980). Lake Bonneville filled the valleys in western Utah to a height of about 1552 m above sea level, with up to 350 m of water, and covered 5,000,000 hectares. The lake existed at the high level for about 3000 years and filled the valleys at lower levels for 10,000 years. We found that most breeding sites of *S. intermontanus* occurred in areas that were inundated by Lake Bonneville and that many of these sites were associated with permanent springs. This study extends some of the earlier observations that are unique to *S. intermontanus*, describes the breeding habitat, and interprets these observations in terms of the Holocene history of the Bonneville Basin.

METHODS AND MATERIALS

Chemical analysis was performed by the Uintex Corporation under contract to the Bureau of Land Management and reported in "Water Inventory for Tooele Range Environmental Statement" for the Salt Lake District Bureau of Land Management (March 1981).

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Under this contract conductivity (corrected to 25 C), pH, dissolved oxygen, alkalinity, arsenic, nitrate, phosphate, suspended dissolved solids, total dissolved solids (residues at 185 C), and coliform bacteria analyses were performed. Duplicate field pH measurements included calibration at each site, with standard buffer solutions of pH 4, 7, and 10 at each site. Conductivity was measured by the YSI-33 portable conductivity meter in both the Uintex Corporation contract and in the springs and water sources outside Tooele County. Climatic information was taken from the United States Climatological Records (U.S. Weather Bureau 1979-1981).

Snout-vent (SVL) measurements were made on tadpoles and adults. Tadpoles were caught with a single net sweep. Measurements of SVL of museum specimens were taken from the collections of Utah Museum of Natural History, University of Utah; Museum of Vertebrate Zoology, University of California at Berkeley; and the Monte L. Bean Life Science Museum, Brigham Young University.

Data for the study reported here were largely collected during the years of 1979, 1980, and 1981. The Bureau of Land Management-contracted water inventory in Tooele County occurred in 1980 and consisted of three trips to the water sources between June and September if water was found on the preceding visits. Photographs of the water sources were taken at each visit.

DESCRIPTION OF THE BONNEVILLE BASIN

The Bonneville Basin, contained within the Great Basin of the Intermountain Region, is typical of the basin and range topography common to western Utah and Nevada. The higher mountains vary from 3050 and 3980 m above sea level and, except for the Wasatch Mountains on the eastern margin, generate few perennial streams that reach the basin floor. The basin floors range from 1284 m (historic high level of the Great Salt Lake) to about 1550 m above sea level. Most of the internal mountain ranges do not have permanent streams that reach the valley floors.

Annual average rainfall varies from 12 to 31 cm in the valley floors. In some years the valleys may receive less than 5 cm of rain

(Hood and Waddell 1968, 1969, Stephens and Sumsion 1978, Hood, Price, and Waddell 1969, Bolke and Sumsion 1978, Stephens 1977). Evaporation from large bodies of open water is estimated to vary between 107 and 127 cm per year (Hood and Waddell 1968, Hood, Price, and Waddell 1969). During the three study years of 1979, 1980, and 1981, over 50% of the rain from April to October occurred in May, with very little precipitation in June and July (Fig. 1). The Bonneville Basin is characterized as receiving spring rains (Kay 1982).

Air temperatures vary between -24 C and -35 C in January and February to the high values of 39 C and 42 C in summer. Freezing temperatures can be expected from October through April. A large portion of the Bonneville Basin has 120 frost-free days annually. Soil temperatures at Salt Lake City (1290 m above sea level) vary from 0 C to 35 C at a depth of 10 cm and 2 C to 25 C at a depth of 100 cm (U.S. Weather Bureau 1979-1981).

The Bonneville Basin valleys contain four major vegetative types: (1) salt desert, (2) shadscale (*Atriplex confertifolia*), (3) sagebrush (*Artemisia tridentata*)-grass, and (4) pinyon-juniper. Greasewood (*Sarcobatus vermiculatus*) occupies much of the valley floor and areas adjacent to springs and is sometimes considered a wetlands indicator species. Sagebrush-grass occurs in the eastern Bonneville Basin and in Nevada, and is not widely distributed in the Bonneville Basin. Pinyon-juniper lower elevational limits occur between 1600 and 1800 m above sea level (West et al. 1978). *Atriplex* is the most prevalent vegetative type that occupies the desiccated valleys of the Bonneville Basin and is undergoing evolutionary change by chromosome polyploidy and interspecific hybridization (Stutz et al. 1979). The general terrestrial ecology of the Bonneville desert was described by Fautin (1946). Within the Bonneville Basin eight mountain ranges occur that contain boreal associations.

RESULTS

BONNEVILLE BASIN AQUATIC RESOURCES.—In the south central portion of the Bonneville Basin, 169 aquatic sites were investigated (Fig. 2). Most of the sites were observed in

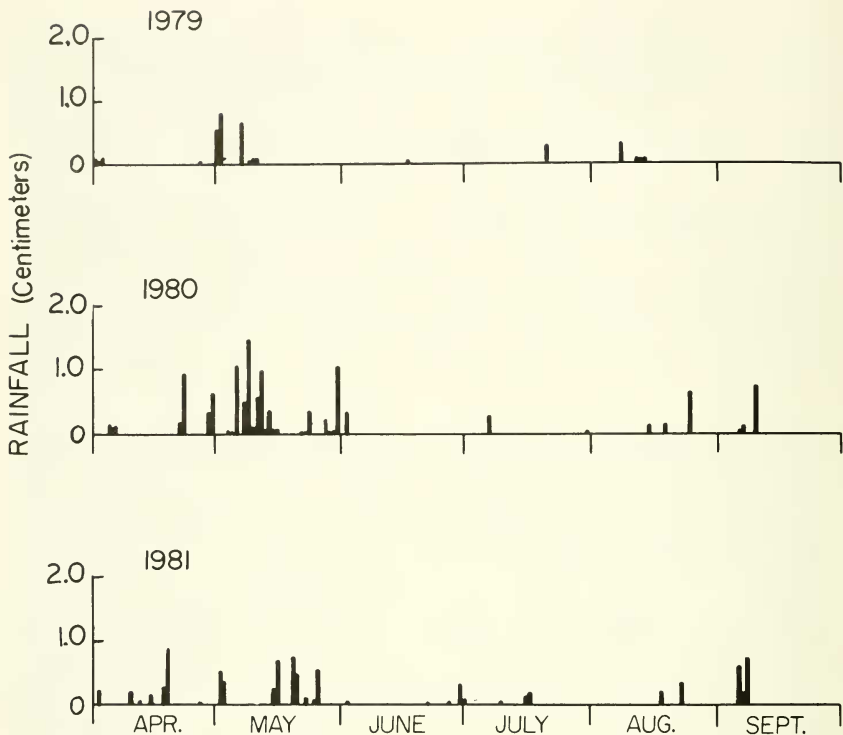


Fig. 1. Precipitation records for Dugway, Utah ($40^{\circ} 11'$ North and $112^{\circ} 56'$ West) during the active season of the spadefoot toad (*S. intermontanus*). Data modified from the U.S. Weather Bureau Climatological Records for 1979, 1980, and 1981.

1980, but some sites in Whirlwind and Skull valleys were observed for three years. Of these 169 sites, 51 were used by *S. intermontanus* at least one of the three years. Browns Spring was utilized only one year in five years of observations. The sites varied in size from small seeps (0.08 m^2 by 10 cm deep) to large reservoirs with over 1200 m^3 of water.

The aquatic resources utilized by spadefoots consisted of man-made reservoirs (57%) and springs (43%). The man-made reservoirs formed water sources where none previously existed and can be characterized as having widely fluctuating volumes of water. It is common for a reservoir to be full one year and empty the next year due to the nature of the precipitation patterns. Even when filled

during the spring and early summer, water is usually evaporated by autumn. The runoff-filled reservoirs pick up chemicals from the soil and wind-blown particles (including saline dust) over the watershed, or from the bentonite lining of the reservoirs (Stephens and Sumsion 1978).

The springs utilized by the spadefoots were temporary or permanent. The portion of the springs utilized by spadefoots were the associated reservoirs (59%), water troughs (27%), streambeds (5%), and wetlands (42%). The wetlands utilized consisted of the distal end of a natural spring (14%), small seeps (14%), or a spring that was dug out (14%). Often spadefoots bred in the reservoir, water trough, and spring at a given site—thus accounting for more than 100% values. If a

series of reservoirs were associated with a spring, the spadefoots bred in the most distal reservoir. Although many of the utilized springs had permanent water, usually the water levels declined by summer to the point a littoral zone could not form. Successful breeding sites were characterized by the absence of aquatic plants in some portion of the aquatic resource.

The elevational distribution of the water sources is shown in Figure 3. Of the total water sources that were utilized by *S. intermontanus*, 74% of the sites were below 1550 m elevation or the height of former Lake Bonneville. Only 27% of the nonutilized sites were below the 1550 m elevation. Less than 14% of the utilized water sources were within the pinyon-juniper region (above 1600 m). The highest elevation spring (2012 m) was utilized by chorusing spadefoots that never bred.

The pH of the water sources utilized by the spadefoots varied from 7.2 to 10.4, with most of the sources having a pH of 8 to 10. Although 84% of the springs contained water with pH of less than 8, the wetlands of these springs often contained water with pH greater than 8. Most of these water sources contained less than 1000 mg/l of total dissolved solids, although Browns Spring contained up to 4800 mg/l.

Under evaporating conditions, phosphate, nitrate, and pH behaved in an unpredictable manner, sometimes increasing and sometimes decreasing in concentration. Alkalinity and total dissolved solids tend to concentrate in a linear manner. No chemical concentrated in direct proportion to the volume—that is, if the volume decreased by a hundredfold, the chemical concentration in many instances did not even increase by tenfold. Often dead tadpoles could be observed in dried-up reservoirs.

ADULT EMERGENCE AND BREEDING.—Although rainfall or the low-frequency sounds of rain falling on the ground are considered stimuli for emergence and breeding for *S. couchi* and possibly for *S. multiplicatus* (Dimmitt and Ruibal 1980b), the stimuli for emergence and breeding of *S. intermontanus* in the Great Basin is unknown. Breeding occurs in April, May, and early June in the Bonneville Basin, where the spring rains can be

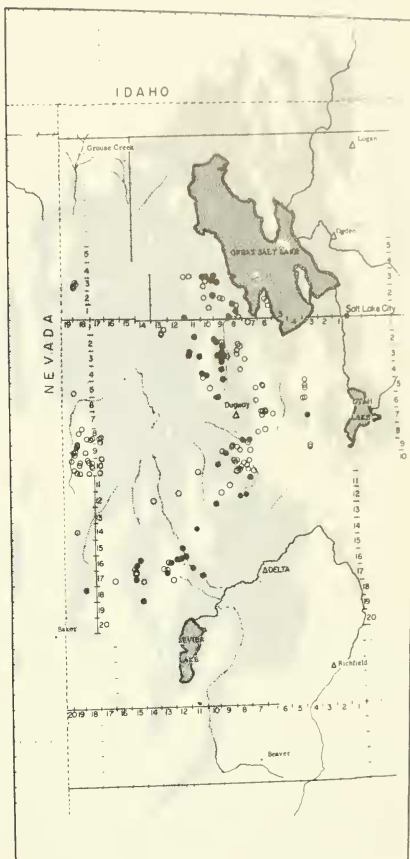


Fig. 2. Breeding sites of the spadefoot toad (*S. intermontanus*) in the Bonneville Basin of the Great Basin. The light shaded area is the extent of former Lake Bonneville according to Synder, et al. (1964). Vertical series of numbers refer to the township number, and the horizontal series of numbers refer to the range. The diameter of each circle represents approximately 5 km. Open circles: water sources not utilized by spadefoots. Closed circles: water sources utilized by breeding spadefoots.

characterized as generalized and gentle (compared to the localized, torrential rains of late summer). In 1981 five rainfalls were observed from the middle of April (which stimulated the breeding) to the end of May (Fig. 1). At White Rocks seep in Skull Valley, the breeding occurred in the middle of April and

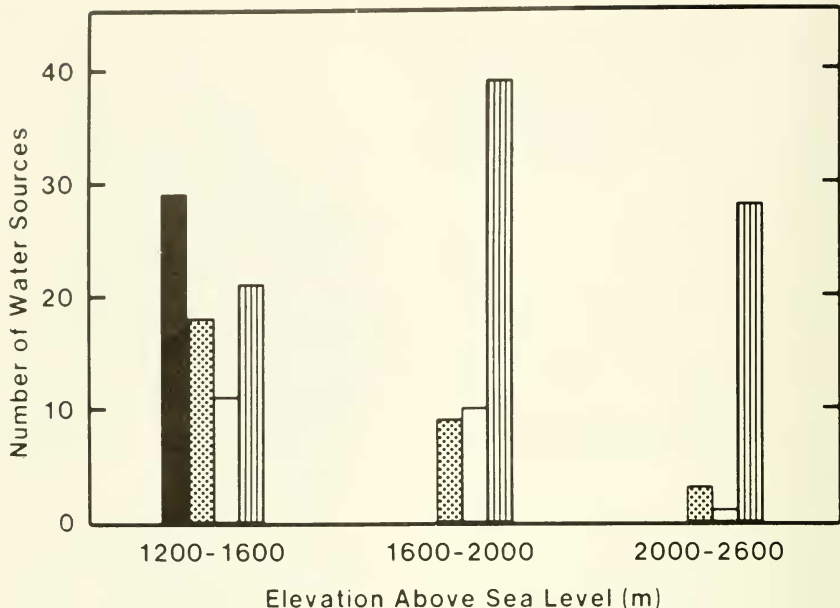


Fig. 3. Distribution of water sources with respect to elevation above sea level. Solid pattern: ephemeral stream-filled reservoirs that were utilized by *S. intermontanus*. Stippled pattern: ephemeral stream filled reservoirs not utilized by spadefoots. Open pattern: springs utilized by breeding spadefoots. Vertical line pattern: springs not utilized by spadefoots.

again at the end of May after a flash flood scoured the seep. In Tule Valley spadefoots bred in South Tule Spring in April and at the end of May in nearby Painter Spring. It would seem that, if the mid-April rain stimulated the spadefoots to breed, then they would be stimulated to breed four additional times before the end of May.

Conversely, at the end of May one spring contained at least two chorusing spadefoots. No rain had fallen for the previous several days, and the chorusing activity occurred for at least three consecutive evenings without any additional rainfall. Although the general initial breeding seems to be stimulated by rainfall at most sites, exceptions are noted.

TADPOLE OBSERVATIONS.— Tadpole growth rates at six different springs are shown in Figure 4. The initial growth rates varied from 0.53 to 0.66 mm SVL per day at the six springs. If there was abundant water in June, the tadpole growth rate slowed down (see

White Rock Spring in Fig. 4). Most metamorphosis occurred by early July. The sizes of the toadlets at metamorphosis varied from 16 to 38 mm SVL.

Tadpoles were found in four springs during August and September. Slower initial growth rates at Henry Spring water trough (Fig. 4) may be responsible for the occurrence of tadpoles in August. Chemical analysis of the springs in Figure 4 varied, with total dissolved solids from 200 mg/l at White Rocks to 2070 mg/l at Eight Mile Spring. Henry Spring was similar to Eight Mile Spring. The population that was observed at Browns Spring in September was probably frozen before metamorphosis could take place. At the time of metamorphosis in August at Henry Spring, numerous dead toadlets were observed near the water.

ADULT SIZE.— At Painter Spring water trough in Tule Valley adult spadefoots were actually observed breeding in 1981. The

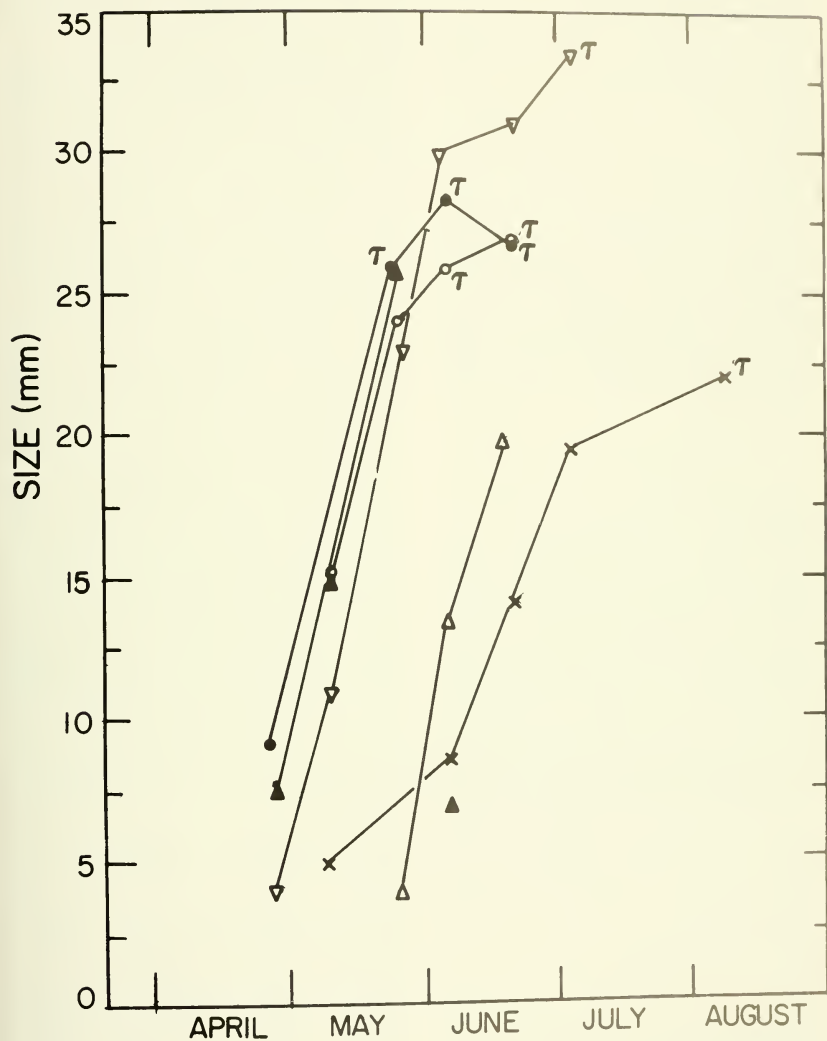


Fig. 4. Tadpole (*S. intermontanus*) growth rates in different springs. The tadpole length (snout-vent length) was measured. ▲, White Rocks seep; x, Henry Spring; ▽, White Rocks Spring; ○, Eight Mile Spring; △, Painter Spring; and ●, South Tule Spring. Metamorphosing tadpoles (with four legs and tail) or toadlets present are indicated by Tau. The tadpoles were caught with a single sweep of the net, measured, and the average size shown in the figure.

average size (SVL) of the nine individuals was $67 \text{ mm} \pm 6.7$ (range, 57 to 77 mm). Because of the large size of these spadefoots compared to values in the literature, the collections representing 10 locations in the Bonneville Basin as well as all the other *S. intermontanus* in the Great Basin were measured. Statistical data are shown in Table 1. The specimens from the Bonneville Basin were larger ($58 \pm 5.3 \text{ mm}$) compared to those specimens from the Colorado River Basin of Utah ($52 \pm 4.8 \text{ mm}$), Idaho ($49 \pm 3.9 \text{ mm}$), Nevada ($49 \pm 4.1 \text{ mm}$), or Washington, Wyoming, Oregon, and Arizona. Both the Bonneville Basin ($z = +6.7$) and the Humboldt River Basin in Nevada ($z = -4.9$) have populations of spadefoots whose mean size exceeds the 99% confidence intervals of the total population, indicating that the size difference is real.

DISCUSSION

Scaphiopus intermontanus utilizes every type of water source for breeding in the Bonneville Basin as long as the total dissolved solids are less than 5000 mg/l. Breeding can occur in permanent reservoirs that contain an abundance of vegetative growth, but under these conditions tadpoles may not survive to metamorphosis. The highly successful breedings took place in water sources that either desiccated during the summer or had a large

draw-down of water (in which case a littoral zone of vegetative growth was lacking), or breeding occurred in stream beds scoured by flash floods. Only 8% of the water sources were entirely natural. Humans, through range improvements, have created new habitat in the Bonneville Basin for the spadefoots and this new habitat greatly reflects typical breeding habitat of the genus *Scaphiopus*. Some of these new water sources are over 15 km from any existing water sources and, to utilize these sources for breeding, the spadefoots must disperse overland. Although human-made reservoirs are widely utilized, during the 1979 limited rainfall (Fig. 1), permanent springs were utilized in Whirlwind Valley because the reservoirs were without water. Subsequent years (1980, 1981) the reservoirs were utilized and the springs were vacated. The lack of large water sources and the sparseness of the water sources in general would not be conducive to large numbers of breeding adults.

The stimulus by which spadefoots emerge and breed has been the low-frequency sounds of rain falling on the ground and not moisture per se (Dimmitt and Ruibal 1980b). Linsdale (1938) was the first to note that spadefoots may breed without the stimulus of rainfall and suggested such several other stimuli as flash flooding and other chorusing spadefoots. Observations in the Bonneville Basin confirm that not all breeding occurs

TABLE 1. Variations in snout-vent length (SVL) of adult spadefoot toads (*Scaphiopus intermontanus*) in the Great Basin. Z is the measure of confidence interval and equals the deviation from the mean divided by the standard deviation of the subpopulation mean. If Z is between -2.58 and +2.58, then there is a 99% confidence that the normal distribution of the total population contains the subpopulation mean.

AREA	NUMBER	MEAN SIZE (SVL-MM)	STANDARD DEVIATION)	Z
TOTAL	254	51	5.1	
UTAH	114	53	5.4	4.1
Bonneville Basin	28	58	5.3	6.6
Colorado River Drainage	77	52	4.8	2.1
ARIZONA (Cocconino County)	8	54	3.2	1.1
IDAHO	26	49	3.9	-2.1
NEVADA	87	49	4.1	-4.5
Humboldt Drainage	55	48	6.7	-4.9
Western	11	52	5.6	0.7
Southern	21	49	4.7	-1.9
OREGON	12	50	3.3	-0.7
WASHINGTON	5	48	3.7	-1.3
WYOMING (+ Daggett County, Utah)	5	52	4.7	0.4

with rainfall, although rainfall may be the main stimulus. Conversely, if rainfall is the main stimulus, not all comparable rainfalls stimulate breeding. Both of these observations may be explained by the postbreeding dispersion of the spadefoots and the scarcity of water sources for breeding. If, for instance, the spadefoot is 5 km from a water source when it hibernates, the first rainfall may cause emergence. The travel time for the spadefoot to reach a water source may be from several days to a month, if a water source is to be reached during the breeding season. Consequently, a delayed response between rainfall and breeding may occur.

Until the historic development of water sources for range management, the water sources in many valleys (west of the Cedar Mountains, Whirlwind Valley, and Puddle Valley) were nonexistent. Furthermore, the rainfall patterns in the Great Basin are diverse, with precipitation peaks in winter (California), spring (central Nevada, Idaho, and Bonneville Basin), and summer (Colorado Plateau) (Kay 1982). These conditions have probably existed in the Great Basin for 4500 years, since the establishment of the present ecosystem (Wells 1983). If spadefoots were to adapt to the cold desert ecosystem in the Great Basin, they would have to have adapted to sparse aquatic breeding habitat, to utilization of flowing spring snowmelt streams, and to spring breeding (tadpoles would not metamorphose in time for July and August breeding).

Upon desiccation of Lake Bonneville, new terrestrial habitat was formed. *Atriplex* evolved with many new polyploid forms and with hybridization (Stutz et al. 1979) and was fully adaptive to this new basin environment. Pinyon-juniper (*Pinus monophylla* and *Juniperus osteosperma*) invaded the region from the southern refugium (Wells 1983), and the monotypic subalpine bristlecone pine (*Pinus longaeva*) forest disappeared from the 1660-m elevation level about 10,000 years ago. During the pluvial era, the subalpine forest and the sagebrush approached the lake level (Wells 1983, Currey and James 1982).

During the pluvial era, *S. internontanus* was isolated on some island ranges or in sand dune regions like the Escalante Desert in southern Bonneville Basin. Sand dunes were

habitat for the relict diploid *Atriplex canescens* (Stutz et al. 1975) and could have furnished the necessary aquatic habitat for spadefoots adjacent to Lake Bonneville. A second possibility is that the spadefoots were in the Mohave refugium along with the pinyon-juniper and migrated north in post-pluvial times.

The significance of the larger snout-vent length of the Bonneville Basin spadefoot population could be (1) genetic isolation of small populations during the 3000-year Lake Bonneville period; (2) adaptations for longer periods of hibernation (Jones 1980, Dimmitt and Ruibal 1980a), which would be required during the more xeric conditions that existed in the Bonneville Basin (Currey and James 1982); (3) more food energy going to increase size instead of reproductive potential because spadefoots may not breed every year, apparently because of water scarcity; or (4) reduced adult predation in the Bonneville Basin, which creates older populations.

Scaphiopus internontanus is not expected to acquire new responses to environmental conditions in the Great Basin in general and the Bonneville Basin in particular in view of the numerous restraints placed on the habitat with respect to precipitation, water sources, and biogeographical changes during the Holocene era. Although *S. internontanus* gives the appearance of becoming more amphibianlike in its behavior (not responding to precipitation and breeding in permanent water), it certainly has adapted to humanly developed typical *Scaphiopus* habitat in the Bonneville Basin. No other amphibian was found in the 151 water sources inventoried with the exception of the Western Spotted Frog (*Rana pretiosa*), which utilized the permanent portion of the Tule Valley springs.

ACKNOWLEDGMENTS

The authors wish to thank Dr. R. Ruibal (Department of Biology, University of California at Riverside), Dr. D. Currey (Department of Geography, University of Utah), and Dr. J. S. Gates (Water Resources Division, U.S. Geological Survey, Salt Lake City) for critically reviewing the initial manuscripts; and Dr. P. Kay (Department of Geography, University of Utah) for assistance with the

statistical analysis of the adult spadefoot specimens. Further thanks are given to Dr. Harry W. Greene (Museum of Vertebrate Zoology, University of California at Berkeley), Dr. D. Cox (Monte L. Bean Life Science Museum, Brigham Young University, Provo, Utah), and Dr. J. Legler (Utah Museum of Natural History, University of Utah) for making available the specimens of spadefoot toads.

LITERATURE CITED

- BLAIR, W. F. 1956. Mating call and possible stage of speciation of the Great Basin spadefoot. *Texas Journal of Science* 8:236-238.
- BOLKE, E. L., AND C. T. SUMSION. 1978. Hydrologic reconnaissance of the Fish Springs Flat area, Tooele, Juab, and Millard counties, Utah. State of Utah Dept. Nat. Res., Division of Water Rights Tech. Publ. no. 64.
- BRAGG, A. N. 1961. A theory of the origin of spadefooted toads deduced principally by a study of their habits. *Animal Behavior* 9:178-186.
- CURREY, D. R. 1980. Coastal Geomorphology of Great Salt Lake and Vicinity. Utah Geological and Mineral Survey, Bulletin 116:69-82.
- CURREY, D. R., AND S. R. JAMES. 1982. Paleoenvironments of the northeastern Great Basin and north-eastern basin rim region: a review of geological and biological evidence. Pages 27-52 in D. B. Madsen and J. F. O'Connell, eds., *Man and environment in the Great Basin*. Society for American Archeology, Paper 2.
- DIMMITT, M. A., AND R. RUBAL. 1980a. Exploitation of food resources by spadefoot toads (*Scaphiopus*). *Copeia* 1980:854-862.
- . 1980b. Environmental correlates of emergence in spadefoot toads (*Scaphiopus*). *J. Herpetology* 14:21-29.
- FAUTIN, R. W. 1946. Biotic communities of the northern desert shrub biome in western Utah. *Ecological Monographs* 16:251-310.
- HARDY, R. 1938. An annotated list of reptiles and amphibians of Carbon County, Utah. *Utah Acad. Sci., Arts, Letters* 15:99-102.
- HOOD, J. W., D. PRICE, AND K. M. WADDELL. 1969. Hydrologic reconnaissance of Rush Valley, Tooele County, Utah. State of Utah Dept. Nat. Res., Division of Water Rights Tech. Publ. 23.
- HOOD, J. W., AND K. M. WADDELL. 1968. Hydrologic reconnaissance of Skull Valley, Tooele County, Utah. State of Utah Dept. Nat. Res., Division of Water Rights Tech. Publ. 18.
- . 1969. Hydrologic reconnaissance of Deep Creek Valley, Tooele and Juab counties, Utah, and Elko and White Pine counties, Nevada. State of Utah Dept. Nat. Res., Division of Water Rights Tech. Publ. 24.
- JONES, R. M. 1980. Metabolic consequences of accelerated urea synthesis during seasonal dormancy of spadefoot toads, *Scaphiopus couchii* and *Scaphiopus multiplicatus*. *J. Experimental Zool.* 212:255-267.
- KAY, P. A. 1982. A perspective on Great Basin paleoclimates. Pages 76-81 in D. B. Madsen and J. F. O'Connell, eds., *Man and environment in the Great Basin*. Society for American Archeology, Paper 2.
- LA RIVERS, I. 1942. Some new amphibian and reptile records for Nevada. *J. Entom. and Zool.* 34:53-68.
- LINSDALE, J. 1938. Amphibians and reptiles in Nevada. *Amer. Acad. Arts and Sci. (Daedalus)* 73:197-257.
- . 1938. Environmental response of vertebrates in the Great Basin. *Amer. Midland Nat.* 19:1-206.
- STEPHENS, J. C. 1977. Hydrologic reconnaissance of the Tule Valley Drainage Basin, Juab and Millard counties, Utah. State of Utah Dept. Nat. Res., Division of Water Rights Tech. Publ. 56.
- STEPHENS, J. C., AND C. T. SUMSION. 1978. Hydrologic reconnaissance of the Dugway Valley-Government Creek Area, West-Central Utah. State of Utah Dept. Nat. Res., Division of Water Rights Tech. Publ. 69.
- STUTZ, H. C., J. M. MELBY, AND G. K. LIVINGSTON. 1975. Evolutionary studies of *Atriplex*: a relic gigas diploid poulation of *Atriplex canescens*. *Amer. J. Botany* 62:236-245.
- STUTZ, H. C., C. L. POPE, AND S. C. SANDERSON. 1979. Evolutionary studies of *Atriplex*: adaptive products from the natural hybrid, 6N *A. tridentata* and 4N *A. canescens*. *Amer. J. Botany* 66:1181-1193.
- SYNDER, C. T., G. HARDMAN, AND F. F. ZDENEK. 1964. Pleistocene lakes in the Great Basin. U.S. Geological Survey.
- SYNDER, J. O. 1920. *Scaphiopus* in northern Nevada. *Copeia* 1920:83-84.
- TANNER, V. M. 1931. A synoptical study of Utah amphibian. *Utah Acad. Sci., Arts, and Letters* 8:159-198.
- U.S. WEATHER BUREAU. 1979-1981. Climatologic data, Utah. Vol. 81-83. National Climatic Center, Asheville, North Carolina.
- WELLS, P. V. 1983. Paleobiogeography of montane islands in the Great Basin since the last glaciopluvial. *Ecological Monographs* 53:341-382.
- WEST, N. E., R. J. TAUSCH, K. H. REA, AND P. T. TUELLER. 1978. Phytogeographical variation within Juniper-Pinyon woodlands of the Great Basin. *Great Basin Nat. Mem.* 2:119-136.
- WOOD, W. F. 1935. Encounters with the western spadefoot, *Scaphiopus hammondi*, with a note on a few albino larvae. *Copeia* 1935:100-102.
- WRIGHT, A. H., AND A. W. WRIGHT. 1949. *Handbook of frogs and toads*. Comstock Publishing Co., Ithaca, New York.